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Leaf to landscape responses of giant sequoia to hotter drought: An introduction and synthesis for the special section☆

Koren R. Nydick[a,*], Nathan L. Stephenson[b], Anthony R. Ambrose[c], Gregory P. Asner[d], Wendy L. Baxter[c], Adrian J. Das[b], Todd Dawson[c], Roberta E. Martin[d], Tarin Paz-Kagan[d]

[a] Division of Resources Management and Science, Sequoia and Kings Canyon National Parks, Three Rivers, CA 93271, United States
[b] U.S. Geological Survey, Western Ecological Research Center, Three Rivers, CA 93271, United States
[c] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, United States
[d] Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305, United States

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ABSTRACT

Hotter droughts are becoming more common as climate change progresses, and they may already have caused instances of forest dieback on all forested continents. Learning from hotter droughts, including where on the landscape forests are more or less vulnerable to these events, is critical to help resource managers proactively prepare for the future. As part of our Leaf to Landscape Project, we measured the response of giant sequoia, the world's largest tree species, to the extreme 2012–2016 hotter drought in California. The project integrated leaf-level physiology measurements, crown-level foliage dieback surveys, and remotely sensed canopy water content (CWC) to shed light on mechanisms and spatial patterns in drought response. Here we summarize initial findings, present a conceptual model of drought response, and discuss management implications; details are presented in the other four articles of the special section on Giant Sequoias and Drought. Giant sequoias exhibited both leaf- and canopy-level responses that were effective in protecting whole-tree hydraulic integrity for the vast majority of individual sequoias. Very few giant sequoias died during the drought compared to other mixed conifer tree species; however, the magnitude of sequoia drought response varied across the landscape. This variability was partially explained by local site characteristics, including variables related to site water balance. We found that low CWC is an indicator of recent foliage dieback, which occurs when stress levels are high enough that leaf-level adjustments alone are insufficient for giant sequoias to maintain hydraulic integrity. CWC or change in CWC may be useful indicators of drought stress that reveal patterns of vulnerability to future hotter droughts. Future work will measure recovery from the drought and strengthen our ability to interpret CWC maps. Our ultimate goal is to produce giant sequoia vulnerability maps to help target management actions, such as reducing other stressors, increasing resistance to hotter drought through prescribed fire or mechanical thinning, and planting sequoias in projected future suitable habitat, which may occur outside current grove distributions. We suggest that managers compare different types of vulnerability assessments and combine vulnerability maps with other sources of information to inform decisions.

1. Introduction

As climate change progresses, policy makers and resource managers will be increasingly challenged to decide how and where to invest scarce resources to address conservation needs. The geospatial pattern of climate change vulnerability, including the location of climate change refugia, can help managers prioritize where on the landscape to apply conservation actions (Ashcroft et al., 2009; Glick et al., 2011; Keppell et al., 2015; Klausmeyer et al., 2011; Morelli et al., 2016; Tingley et al., 2014). Model projections of future climate change often are used to drive such vulnerability assessments (Carroll et al., 2015; Thorne et al., 2017), but managers may be hesitant to apply model results when making place-based decisions due to the uncertainties inherent in the models (Gray, 2011; Kujala et al., 2013; Michalak et al., 2017). This has been our experience working with managers in national parks and national forests in the southern Sierra Nevada (Nydick and Sydoriak, 2014).

We propose empirical measurements of drought response as a

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* Corresponding author.
E-mail address: koren_nydick@nps.gov (K.R. Nydick).

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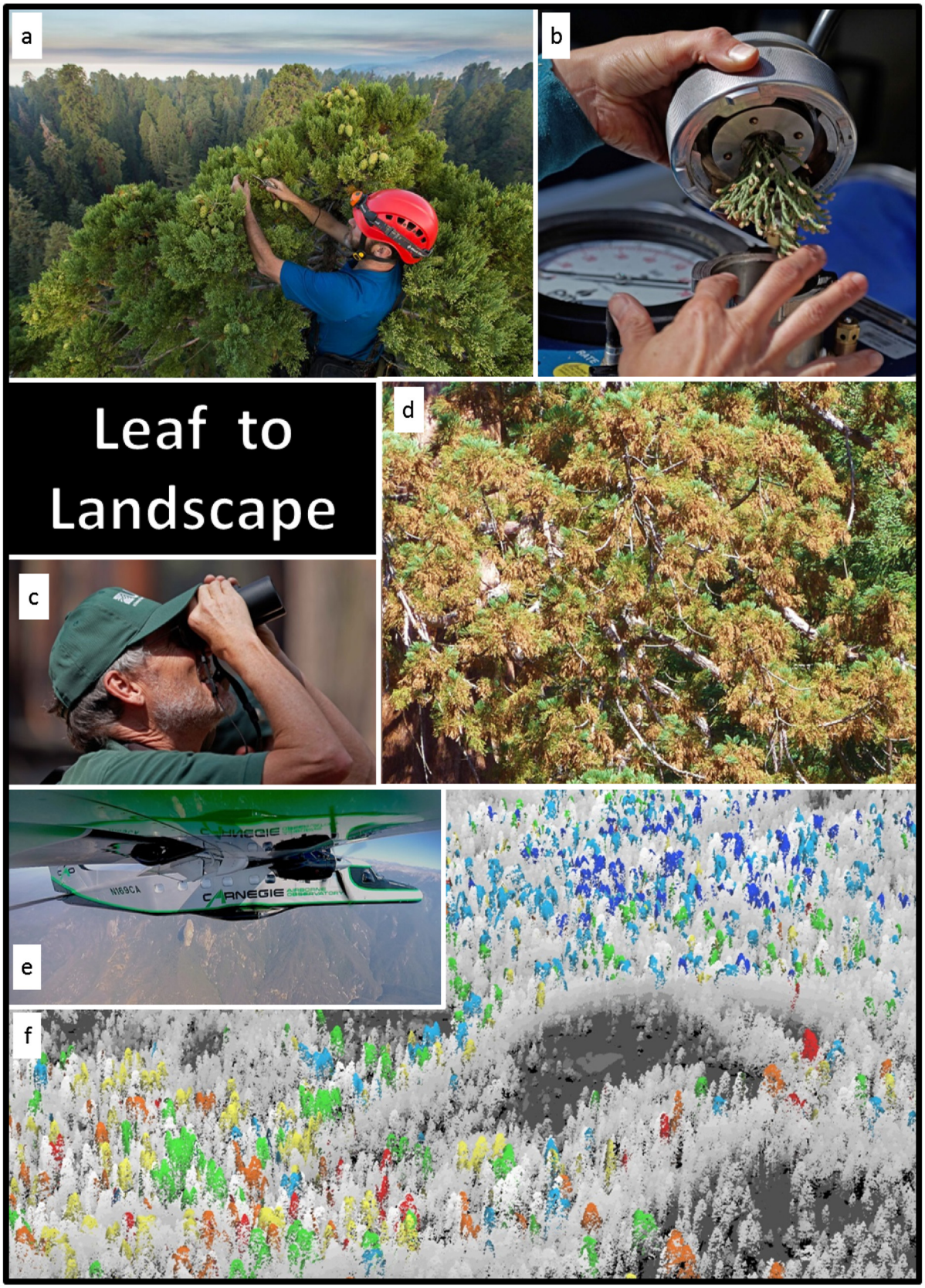

Fig. 1. Leaf to Landscape measurements across three spatial scales. (a and b) Climbers collected giant sequoia foliage for leaf-level analyses in 49 trees (photos: Lincoln Else, Anthony Ambrose); (c and d) Surveyors documented percent foliage dieback along trail corridors in eight sequoia groves (photos: Anthony Ambrose, Nate Stephenson); (e) Carnegie Airborne Observatory (CAO) flights captured LiDAR and imaging spectroscopy data across 38 groves (photo: Greg Asner); and (f) canopy water content (CWC) was mapped for giant sequoia crowns (high CWC is blue; low CWC is red; image: Greg Asner). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

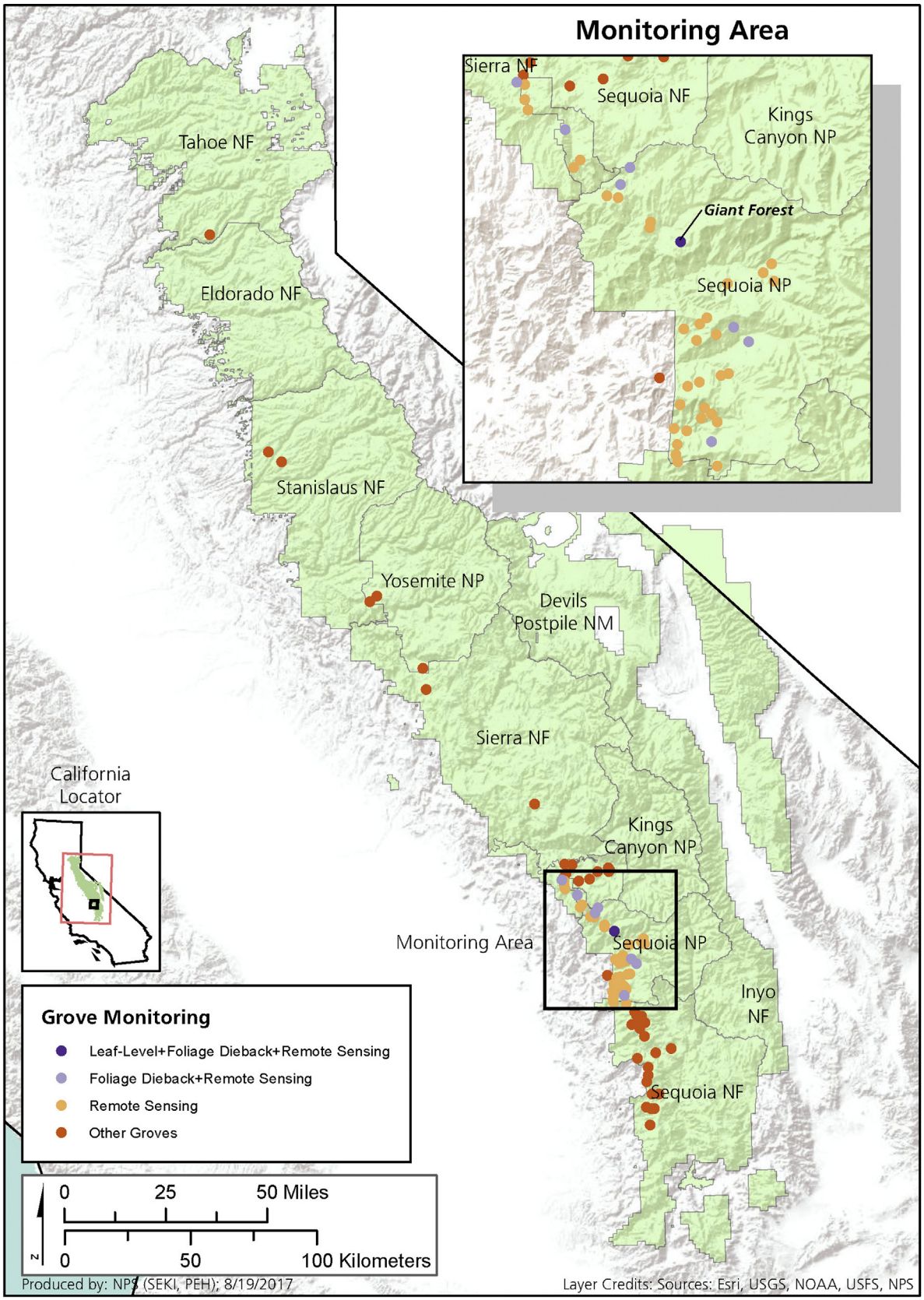

Fig. 2. Map of the Sierra Nevada showing the locations of giant sequoia groves. Thirty-eight groves were analyzed via remote sensing (orange, gray, and blue dots), eight of those groves were additionally surveyed for foliage dieback (gray and blue dots), and 49 individual sequoias within the Giant Forest grove were also climbed for direct physiological measurements (blue dot). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

promising alternative method to map climate change vulnerability for forests (Verbesselt et al., 2016). As temperatures warm, droughts are becoming hotter, which exacerbates the drying effect of reduced precipitation. These "hotter droughts" already are causing forest dieback in many parts of the world and are expected to increase in frequency and severity as temperatures continue to rise (Breshears et al., 2005; Allen et al., 2010; Allen et al., 2015). Hotter droughts provide critical opportunities for scientists and managers to let the trees themselves reveal which parts of the landscape are more or less vulnerable. Resulting vulnerability maps could help managers to strategically target treatments that give forests a better chance to survive future hotter droughts. Currently, such tools are focused on prescribed fire or mechanical thinning, which are used to selectively remove smaller trees and reduce competition for moisture among the remaining trees (van Mantgem et al., 2016).

California's recent hotter drought from 2012 to 2016 was deemed the most severe in at least the ~120 year instrumented record, and potentially much longer (Diffenbaugh et al., 2015; Williams et al., 2015). More than 100 million trees have died (USDA Forest Service, 2016; Young et al., 2017), and many hundreds of millions more underwent substantial desiccation (Asner et al., 2016). While relatively few giant sequoias succumbed to the drought, the relative wetness of sequoia groves declined (Su et al., 2017), and many sequoias experienced unprecedented levels of foliage dieback (Stephenson et al., this issue). As a likely preview of the future, this hotter drought presented an unparalleled opportunity to measure geospatial patterns in the response of giant sequoias and other forest trees (Brodrick and Asner, 2017; Paz-Kagan et al., 2017). We began the "Leaf to Landscape Project" to improve our mechanistic understanding of forest vulnerability to hotter droughts and eventually to produce empirically-derived maps of vulnerability across the landscape.

In this special section, "Giant Sequoias and Drought", we report on preliminary Leaf to Landscape results focusing on the iconic giant sequoia (*Sequoiadendron giganteum* Lindl. [Buchholz]). Giant sequoias are endemic to the Sierra Nevada, and are the largest and among the oldest and tallest tree species in the world (Stephenson, 1996). They have awed and inspired generations of Americans, as well as people from all over the world, and are an economically-important attractant for tourists visiting central California. While giant sequoias have long been considered to have high resistance to fire, insects, and disease relative to other tree species (Hartesveldt et al., 1975; Piirto, 1994), concern about them is heightened because of their social and ecotourism value. They exist mixed with white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and other tree species in ~70 scattered groves totaling about 14,600 ha. These groves, most of which are protected on public lands, occur along a narrow elevation band (1400–2150 m) that generally falls near the historic rain-snow transition where more than 50% of precipitation falls as snow (York et al., 2013). While they are resistant and resilient to climate change in certain ways, sequoias also have traits that suggest vulnerability (York et al., 2013). A potential "Achilles heel" in terms of susceptibility to hotter droughts is the sequoias' enormous demand for water, with a single mature tree using more than 2000 L of water per summer day (Ambrose et al., 2016). Additionally, giant sequoias have relatively low genetic diversity compared to other tree species and this may limit their ability to adapt to new conditions (Dodd and DeSilva, 2016; Fins and Libby, 1994).

2. Methods

All methods are discussed in detail within the four other papers of this special section. Here we offer a brief, integrated overview.

2.1. The leaf to landscape approach

The Leaf to Landscape Project seeks to understand effects of hotter drought on giant sequoias by integrating measurements across three spatial scales: (1) leaf-level water status and physiology; (2) foliage dieback along trail corridor segments; and (3) landscape-scale remote sensing (Figs. 1 and 2). The approach for studying giant sequoia at each of these three spatial scales is summarized below.

2.2. Leaf-level water status and physiology

We selected 49 adult trees and 30 seedlings representing a gradient of foliage dieback in Giant Forest (Sequoia National Park) based on dieback patterns observed in 2014 (Stephenson et al., this issue). During summers 2015 and 2016, tree climbers collected small branches from the sequoia crowns during both pre-dawn and mid-day sampling events. Water potentials were measured soon after with a portable pressure chamber. In the laboratory we analyzed foliage samples for leaf water content, percent carbon and nitrogen, carbon stable isotopic ratio ($\delta^{13}C$), non-structural carbohydrates, cellulose, hemi-cellulose, and lignin. Leaf and shoot mass per area were calculated based on empirical relationships and measurements of shoot area and dry mass. Environmental conditions were recorded at a central location outfitted with a treetop meteorology station and soil moisture content sensors and with temperature and humidity sensors installed in a subset of the study trees (Ambrose et al., this issue).

2.3. Foliage dieback along transects

In 2014, when foliage dieback was first observed, we conducted binocular surveys to document the proportion of dead foliage visible in large giant sequoias along trail corridor segments in eight sequoia groves, including Giant Forest, in Sequoia and Kings Canyon National Parks, The proportion of dead foliage was estimated using five categories ranging from $< 10\%$ to $> 75\%$ of the tree's total visible crown. Trail segments were approximately 150 m wide (75 m on each side) and averaged 6 ha in area (range: 1–24 ha). In 2014, we observed a total of 4278 trees along 144 trail segments. In 2015, we resurveyed nearly all of the same trail segments. In 2016 and 2017, we resurveyed only the trail segments within the Giant Forest grove. All surveys were conducted in September or October after the dead foliage had clearly turned color (Stephenson et al., this issue).

2.4. Landscape-scale remote sensing

In August 2015 and July 2016, we flew the Carnegie Airborne Observatory aircraft outfitted with high fidelity imaging spectroscopy (HiFIS) and light detection and ranging (LiDAR) systems to collect data from Giant Forest and 37 other sequoia groves encompassing 5783 ha in Sequoia and Kings Canyon national parks and vicinity (Asner et al., 2012). The combination of high spatial and spectral resolutions of the HiFIS enabled us to map the giant sequoia distribution, canopy water content (CWC), and live/dead status at the scale of tree crowns across the study landscape. CWC is the total amount of liquid water in the foliage of a canopy per unit area (Asner et al., 2004) and is broadly correlated with leaf water potential and leaf area, thus serving as an indicator of progressive drought-related stress (Asner et al., 2016; Cheng et al., 2006; Ustin et al., 1998). We also mapped topographic and canopy characteristics derived from digital elevation models (DEMs) based on the LiDAR data and from additional sources of data (Martin et al., this issue; Paz-Kagan et al., this issue).

3. Results and discussion

Giant sequoias exhibited both leaf- and canopy-level responses that appear to have been effective in protecting whole-tree hydraulic integrity during California's hotter drought. Compared to other mixed conifer tree species, very few giant sequoias died during the drought (probably substantially less than 1%; see Stephenson et al., this issue). Sequoias differed in the extent of drought response across the

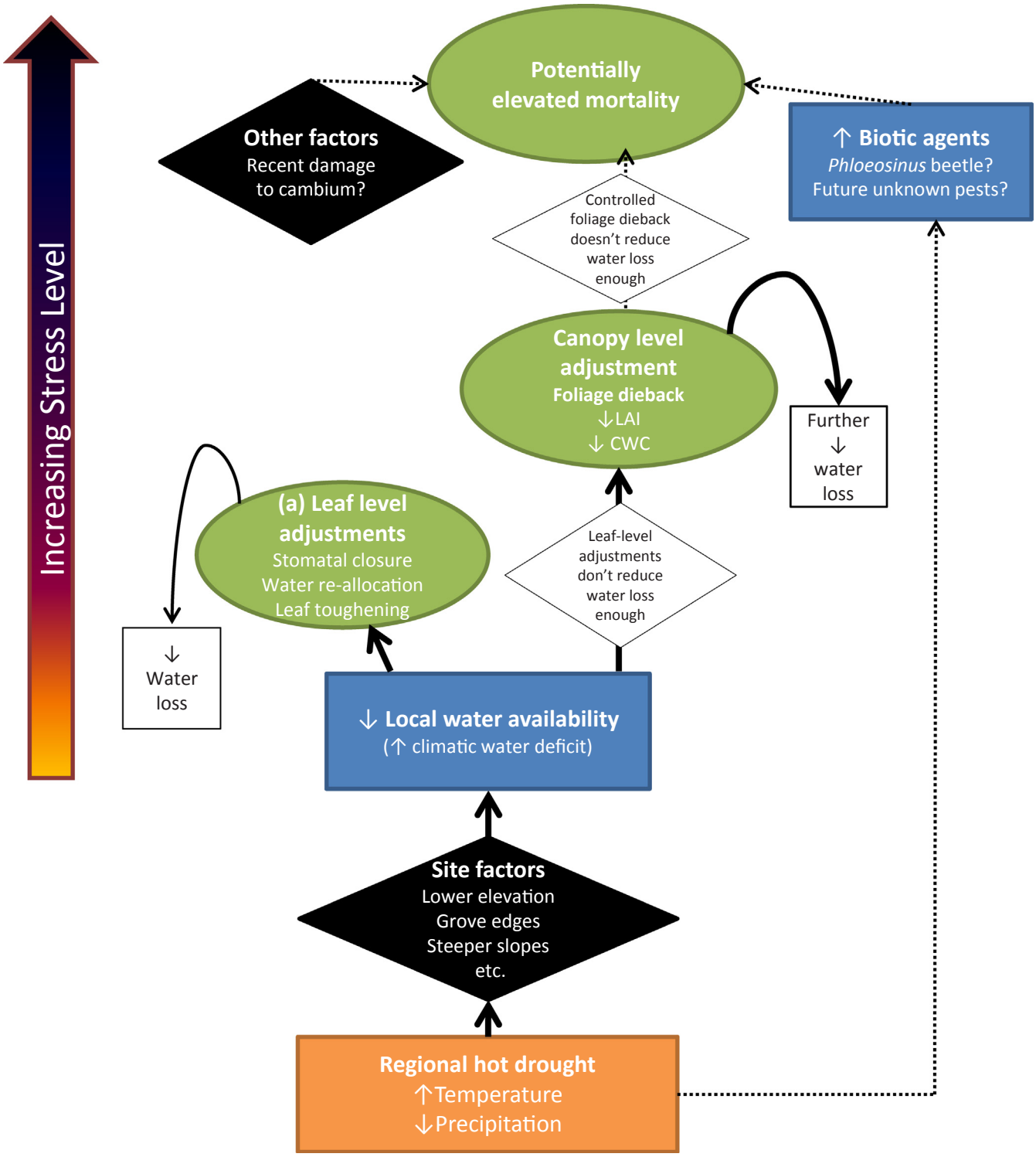

Fig. 3. Conceptual model of giant sequoia response to hotter drought. Dotted lines represent processes for which we have limited observations, while solid lines are supported by strategically collected Leaf to Landscape data (Ambrose et al., this issue; Martin et al., this issue; Paz-Kagan et al., this issue; Stephenson et al., this issue).

landscape, however, and this variability was partially explained by local site characteristics (Fig. 3). Below, we present an overview of findings for the four other papers in this special section (Ambrose et al., this issue; Martin et al., this issue; Paz-Kagan et al., this issue; Stephenson et al., this issue) and present a conceptual model of giant sequoia drought responses.

3.1. Leaf-level water status and physiology

During the drought, water potentials of 49 mature study trees were as low as or lower than any previous measurements made in giant sequoias. The treetop water potentials indicated that some sequoias approached or exceeded several leaf and branch-level physiological thresholds (i.e., leaf turgor loss point, 50% loss in leaf hydraulic conductivity, and air entry point when loss of branch xylem conductivity increases rapidly), signifying that some sequoias were experiencing

unusually high levels of hydraulic stress. Leaf-level adjustments included multiple mechanisms to reduce water loss: increased stomatal closure, redistribution of leaf water to less mobile and longer-term storage, and an increase in recalcitrant leaf cellulose to build tougher, more drought resistant foliage (i.e., leaf toughening) (Fig. 3). Because of the high severity of the drought, however, the capacity for leaf-level compensation in some giant sequoias was apparently overwhelmed and other adjustments, described below, were needed to keep water potentials above the level that would cause widespread hydraulic impairment leading to tree mortality (Ambrose et al., this issue).

3.2. Foliage dieback

In autumn 2014, the single most severe drought year in the 122-year record, many sequoias also made canopy-level adjustments via premature leaf senescence and abscission, meaning that foliage died and was shed, reducing water losses even further. Dieback was much less in 2015, 2016, and 2017, which may mean that foliage loss in 2014 mostly was sufficient to cope with somewhat lessened drought conditions in the following years. Dieback in sequoias was variable both within and among groves and was higher at lower elevations, in areas with lower density of adult sequoias, and on steeper slopes. Although some sequoias experienced > 50% foliage loss, very few died. The small number that died during the drought showed evidence of recent cambial damage from fire and elevated abundance of *Phloeosinus* bark beetles. Causes of mortality are being investigated in our ongoing work. Overall, patterns of foliage dieback suggest that giant sequoia response to drought stress is spatially variable with a significant amount of that variability attributable to water balance site characteristics (Stephenson et al., this issue).

3.3. Landscape remote sensing

For the 49 study trees, correlations between leaf traits (including leaf water content) and CWC were absent or weak. At the scale of Giant Forest, 2015 CWC was related to 2014 foliage dieback, explaining 20% of the variance despite the fact that the CWC incorporated baseline variability in addition to changes that occurred during the drought. These results suggest that CWC is more strongly related to canopy level-changes rather than leaf-level traits (Martin et al., this issue). Canopy water content (CWC) of giant sequoias varied considerably across the 38 groves in a patchy pattern (Fig. 1f). On average, CWC values increased from 2015 to 2016, indicating a general trend of recovery, but this change was variable with some sequoia groves and areas within groves experiencing decreases in CWC. Environmental site characteristics explained 60% of the variability in the change in CWC. We found greater CWC loss at lower elevations, in areas with higher climatic water deficit (CWD) values, in areas with greater distances from water sources, and on steeper slopes. Shorter giant sequoias tended to have greater CWC loss, which contradicts recent findings that larger trees suffer more from drought (Bennet et al., 2015). In addition, giant sequoias growing in areas with lower density of sequoia trees had greater CWC loss. While lower overall mixed-conifer tree density has been linked to reduced levels of drought mortality (van Mantgem et al., 2016; Young et al., 2017), lower density of sequoias likely indicates underlying marginal habitat for the species. This idea is supported by observations at the grove scale; lower CWC values were generally apparent in smaller groves and along the edges of groves (Paz-Kagan et al., this issue).

3.4. Conceptual model of drought responses

Taken together, these results suggest a conceptual model of giant sequoia drought responses that are regulated by environmental site characteristics, occur across a gradient of increasing drought stress, and are potentially synergistic with other stressors (Fig. 3).

Site characteristics mediate the level of water stress experienced by individual sequoia trees and produce non-random patterns in drought response across groves. Drought-stressed sequoias make leaf-level adjustments to reduce water loss, but for some trees these adjustments alone are not enough. Under conditions of more severe drought stress further water conservation is achieved through a controlled process of premature leaf senescence and partial canopy foliage dieback, which reduces leaf area and canopy water content (CWC) in individual trees and at a landscape level. While relatively few giant sequoias died during the recent drought, our observations suggest that drought stress, cambial damage from fire, and elevated abundance of *Phloeosinus* bark beetles may interact to increase mortality risk (Fig. 3).

4. Conclusions and future directions

Our results suggest that remotely sensed CWC and change in CWC may be useful indicators of giant sequoia drought vulnerability that can be measured across landscape scales. As discussed in Section 4 below, there are important management applications for mapping CWC and identifying the site factors and interacting stressors that predispose giant sequoias to elevated drought vulnerability.

Our interpretations of CWC as an indicator of forest vulnerability are preliminary, however, currently based on two remote sensing flights during 2015–2016. Additional work is needed to develop and interpret vulnerability maps with confidence. In the winter of 2016–2017, the Sierra Nevada experienced a return to wet conditions with April 1 snowpack at 163% of multi-decade average for the southern Sierra Nevada (DWR, 2017). Planned analyses of additional remote sensing flights, including data from late summer 2017, and collection of new tree-ring cores from sequoias across a gradient in CWC will enable us to test the link between CWC and drought vulnerability with more confidence. Tree-ring cores will enable us to determine if CWC metrics are a proxy of growth-rate responses to drought, in addition to the foliage dieback we documented in this special section (Stephenson et al., this issue). Remote sensing data from late summer 2017 will help us determine patterns of drought recovery and to characterize baseline CWC under non-drought conditions. Variability in baseline CWC could indicate differences among sites in long-term water availability that drives giant sequoia aboveground biomass and subsequent water demand. The magnitude of change in CWC during a drought may reflect shorter-term water reliability. We hypothesize that the relationship between these two metrics is related to the amount of hydraulic stress that sequoias face during a drought episode, which in turn affects the severity of drought response (Jump et al., 2017). Therefore, understanding the relationship between longer-term baseline CWC and drought-induced changes in CWC is important to interpreting them as indicators of drought vulnerability.

Based on the recent drought, we collected preliminary evidence of lethal hydraulic impairment in the death of small number of giant sequoias, possibly due to interactions of severe drought stress with cambial damage from fire and beetle attack (Stephenson et al., this issue) (Fig. 3). Past research linked basal fire scars to crown damage in giant sequoias and hypothesized water stress as the cause (Rundel, 1973), but did not find evidence that fire scars increase mortality of mature sequoias (Lambert and Stohlgren, 1988). Similarly, *Phloeosinus* bark beetles have been noted in the dead limbs and fallen branches of giant sequoia previously, but were not thought to be mortality agents (Stecker, 1980; Piirto, 1994). We hypothesize that severe drought stress may interact to amplify the effect of these previously non-lethal factors. To strengthen our understanding of the mechanistic link between drought responses and thresholds of giant sequoia mortality, we will continue to identify recently dead sequoias, cause of mortality, and CWC measurements that preceded their death.

Genetic considerations have thus far not been part of our Leaf to Landscape studies; however, mapping of sequoias' genetic variation may reveal additional important aspects of climate change vulnerability

for the species (Erickson et al., 2012). Genetic differences may explain further spatial variation in drought response beyond what we attributed to site characteristics. Spatial patterns of genetic diversity also could play a role in the varied capacity for sequoias to adapt to future conditions over time.

5. Management implications

If upcoming work strengthens support for mapping CWC of giant sequoia as an indicator of drought vulnerability, how could managers apply this information? First, we caution managers about using only one source of information and encourage the use of multiple lines of evidence where possible (Michalak et al., 2017). For example, CWC-based vulnerability maps could be compared with climate model-based projections of vegetation exposure (Thorne et al., 2017) and other remote sensing assessments at coarser scales (Su et al., 2017). Second, there are multiple conceptual approaches to applying vulnerability to decision-making. Managers could opt to minimize risk in the most vulnerable grove areas or they could focus management treatments on low vulnerability areas as the best chance for long-term persistence of the species (Morelli et al., 2016). Alternatively, managers could select a portfolio that includes both higher and lower vulnerability areas to avoid an "eggs in one basket" scenario. In any case, we envision that managers would incorporate other sources of information, such as the locations of other valued resources and the fire and fuels management history of the area, to determine where to apply treatments to achieve multiple goals (Caprio and Lineback, 1997). Importantly, vulnerability assessments don't point to specific decisions, but rather provide a scientific foundation for deliberation. Difficult triage choices will necessarily include social, economic, and legal considerations as well (Glick et al., 2011; Morelli et al., 2016).

What management options do managers have to protect and conserve giant sequoias in the face of climate change and hotter droughts? Managers could work to reduce other stressors that make giant sequoia more susceptible. For example, infrastructure that alters soils and hydrology within and above sequoia groves, including facilities that extract water for human use, could be reduced or eliminated to maximize the moisture available to trees (Demetry and Manley, 2001; NPS, 2017). Managers could thin the forest through managed wildfire, prescribed fire, or mechanical methods to increase resistance to drought mortality (van Mantgem et al., 2016; Boisrame et al., 2017); however, thinning is unlikely to be a panacea if droughts are very severe and/or long in duration. Additionally, based on our observations of severe cambial damage in the low number of trees that died during the recent drought, managers may opt to remove excessive fuel build-up near the bases of selected giant sequoias before applying fire in order to reduce the risk of severe cambial damage interacting with future drought stress. Another option is to consider planting giant sequoias in projected future suitable habitat, which may occur outside current grove distributions (Schwartz et al., 2012). Site characteristics that correspond to low drought vulnerability in the current groves could be incorporated into a model to identify potential future habitat outside of the groves. Managers could choose to collect, conserve, and apply seeds with the intent of capturing the full genetic diversity of giant sequoias in future plantings, or if certain genetic signatures were found to be associated with ability to tolerate hotter droughts, managers could strategically select seed stock more likely adapted to these conditions (Erickson et al., 2012). Regardless of which strategies are selected to conserve giant sequoias in the face of increasingly hotter droughts, it is not certain if these actions actually will help to attain this goal. We suggest that managers track action effectiveness and ecological response in order to promote continual learning and identify when changes in tactics might be needed (Stein et al., 2014).

Given that mapping vulnerability of sequoias to hotter droughts of the future is complex and uncertainties remain in both the tool and its application, why should scientists and managers continue to work towards this goal? First, the threat is real. If temperatures continue to warm and droughts become more frequent, as predicted for the Sierra Nevada, giant sequoias could be at increasing risk from climate-driven shifts in available moisture (Safford et al., 2012; York et al., 2013). Although seemingly invincible on human time-scales, sequoias have been subject to climate-driven shifts and contractions in the past and may have approached extinction during a warm period about 10,000–6000 years ago with their present relative abundance dating back only about 4500 years (Anderson and Smith, 1994; Davis, 1999; Dodd and DeSilva, 2016). Second, as we have shown, not all sequoias will be subject to the same stress levels. While we observed significant stress levels in some giant sequoias, others were seemingly unaffected by the severity of the recent drought. Understanding these patterns is a prerequisite for being strategic in the face of climate change. Third, while giant sequoias garner special attention because of their iconic status, the importance of sequoia groves in terms of adaptation to climate change may ultimately be the role they play in conservation of the Sierra Nevada mixed conifer forest ecosystem in general. Sequoia groves have greater water availability than the surrounding forest and may serve as critical hydrologic refugia for a variety of species (McLaughlin et al., 2017; Rundel, 1972; Su et al., 2017).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.028.

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